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Seasonal, annual and decadal change in tadpole populations in tropical Australian streams

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Abstract. Declines due to fungal disease (chytridiomycosis) have affected many stream-dwelling frog species, especially in the tropics, leading to reduced abundance and diversity of their tadpoles. Studies in the Australian Wet Tropics have demonstrated that some frog species have declined or disappeared, while others have persisted. To assess the occurrence of stream-breeding frogs, we monitored tadpole populations of five frog species in Wet Tropics streams in the early 1990s (uplands, before chytridiomycosis emergence), and in 2011–2013 (uplands and lowlands, after chytridiomycosis emergence), and investigated environmental factors that might influence tadpole abundance. Riffle-dwelling tadpoles of two frog species disappeared from the upland stream site during the 1990s, reflecting reported losses of adult populations. Tadpoles of one upland pool species initially declined but had recovered by 2011–2013. Samples from the lowlands in 2011 to 2013 indicated no similar loss. Chytridiomycosis was the likely cause of changes in tadpole abundances between the two survey periods, given its known occurrence and documented effects on adult frogs in these systems; however, we did not measure its prevalence in this study. Tadpole populations fluctuated seasonally, with abundances highest in spring and summer, reflecting the timing of frog reproduction. The most important biophysical influence on the assemblages that we measured was current velocity. Tadpole peak abundances suggest that they make a substantial contribution at the consumer level of food webs, and that their loss has altered food webs substantially in upland streams.

Keywords: amphibian decline, chytridiomycosis, *Litoria*, *Mixophyes*, recovery, seasonal abundance, wet tropics.

Introduction

Anurans are prominent components of the fauna in freshwater systems, but many species have declined globally over recent decades as a result of the fungal disease chytridiomycosis, caused by the pathogen *Batrachochytrium dendrobatidis* (Richards et al., 1993; McDonald and Alford, 1999; Alford, 2011; Hof et al., 2011). Tadpoles contribute to stream functioning and may influence resource availability and the abundance of other aquatic organisms, thereby influencing food web structure (Colón-Gaud et al., 2009, 2010; Iwai et al., 2009; Frauendorf et al.,

2013; Schmidt et al., 2017). Understanding the habitat requirements and population dynamics of stream tadpoles is an important step towards understanding how they influence the ecology of stream systems, and the effects of their decline; however, stream tadpole population dynamics can be very complex (Alford, 1999) and are poorly known from tropical streams (Bertoluci and Rodrigues, 2002; Eterovick et al., 2010; Strauß et al., 2016). Tadpoles are ideal subjects for surveys of anurans as their entire habitat is available for sampling, whereas stream-breeding adult amphibians may spend considerable time away from the stream (Rowley and Alford, 2007).

Streams are highly variable systems, influenced by seasonal or episodic rainfall, which can rapidly alter flow conditions and substratum composition (Flecker and Feifarek, 1994; Pohlman et al., 2008). Tadpoles select habitats within streams that may be differentially affected by changing flow conditions: they may, for example, use isolated or connected pools,

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runs, riffles or fast-flowing torrents, depending on resource availability and their ability to withstand high current velocities (Inger et al., 1986; Richards, 2002). Tadpole and resultant adult populations may fluctuate as a result of these changing environmental influences. It is important, therefore, to understand seasonal and inter-annual changes in tadpole population sizes and habitat requirements when assessing the status of tadpole populations.

Tadpole population dynamics before and after amphibian declines have been reported for neotropical streams (Lips, 1998, 1999; Hunte-Brown, 2006; Whiles et al., 2006; Colón-Gaud et al., 2010), but there is little published information (Sapsford et al., 2018) for the Australian Wet Tropics bioregion (hereafter “Wet Tropics”). In this region, frogs breed mainly in the warm spring and summer wet season, which is when high flows usually occur, although adult frogs and tadpoles of various developmental stages may be present throughout the year (Richards and Alford, 2005; Cashins, 2009; Sapsford et al., 2013, 2018). Many species of stream-breeding frogs declined or disappeared in the late 1980s to early 1990s, particularly in upland areas (Richards et al., 1993; McDonald and Alford, 1999). The first reported declines coincided with the emergence of chytridiomycosis in the region (Berger et al., 1998; Woodhams and Alford, 2005). However, different species responded differently to the disease: some were eliminated, some survived unchanged, and others recovered following initial declines, despite the continuing presence of the fungus (Woodhams and Alford, 2005; McKnight et al., 2017). High-elevation species were most affected by chytridiomycosis because cool, moist conditions favoured the pathogen’s growth (Johnson et al., 2003; Stevenson et al., 2013), while species with wide elevational ranges were least affected at lower elevations (McDonald and Alford, 1999; McKnight et al., 2017). Infections by *Batrachochytrium dendrobatidis* can produce chytridiomycosis in adult frogs, and can also damage

the mouthparts of tadpoles, affecting development (Blaustein et al., 2005; Cashins, 2009).

We assessed tadpole population dynamics and habitat use, using tadpole abundance data from surveys of an upland stream in 1989–1994, during which large-scale frog declines that were ultimately found to have been caused by chytridiomycosis were reported (Richards et al., 1993; McDonald and Alford, 1999; McKnight et al., 2017), and surveys of upland and lowland streams in 2011–2013. The combined records allowed analysis of habitat requirements and short- and long-term changes in species occurrence and population densities. Prevalence and intensity of infections by *B. dendrobatidis* were not measured during this study, having been the subject of substantial previous work (Berger et al., 1998; McDonald and Alford, 1999; Woodhams and Alford, 2005; additional work reviewed in McKnight et al., 2017). In accordance with this body of work we discuss outbreaks of chytridiomycosis as a likely cause of the declines that we observed in some species.

Materials and methods

Study region and sampling sites

The climate of the Wet Tropics is seasonal tropical, with a distinct wet season during the summer months (November–March). Heavy monsoon rains, often associated with cyclonic activity, cause spates in the streams during this time. During base flow, three major habitats are prevalent: pools, usually ~0.5–1.0 m deep and with negligible current at the surface ($<0.05\text{ ms}^{-1}$); runs, less than 0.8 m deep with distinct but non-turbulent water flow ($0.05\text{--}0.2\text{ ms}^{-1}$); and riffles, usually shallow with swift turbulent flow ($>0.2\text{ ms}^{-1}$). The distinctions between these categories became less evident following heavy rain, when depth increased and flow became fast and turbulent across habitats.

We collected tadpoles from upland streams in the Paluma Range National Park, towards the southern end of the Wet Tropics, and lowland streams in the Tully area further north (supplementary fig. S1). There were two survey periods: 1989–94 and 2011–13. One stream at Paluma, Birthday Creek (18.98°S , 146.17°E , 795 m elevation), was sampled during the first survey period (1989–94). During the second period (2011–13), we collected samples in all the streams: Birthday Creek and Little Birthday Creek (also referred to as Camp Creek, 18.97°S , 146.17°E , 766 m) at Paluma, and two unnamed streams flowing into the Tully River (Stream 1, 17.77°S , 145.65°E , 102 m; and Stream 2,

Table 1. Stream characteristics at Paluma and Tully, 2011–2013. Values were averaged from 3 pools and 3 riffles in each stream. Canopy cover, leaf cover and algal cover were visually estimated at each site and the median percentage range shown. The substratum composition was also visually estimated and substratum size distribution is presented as % of sand/gravel, cobbles and boulders. Ranges represent minimum–maximum values recorded. FRP = Filterable Reactive Phosphorus.

Stream characteristics	Birthday Creek		Little Birthday Creek		Tully Stream 1		Tully Stream 2	
	Pool	Riffle	Pool	Riffle	Pool	Riffle	Pool	Riffle
Current velocity (ms^{-1})	0.0–0.09	0.24–1.30	0.00–0.07	0.05–1.30	0.00–0.45	0.25–2.03	0.00–0.41	0.37–1.85
Canopy cover at > 10 m (%)	25–50	25–50	75–100	25–50	0–25	0–25	25–50	0–25
Leaf cover (%)	50–75	0–25	50–75	0–25	0–25	0–25	0–25	0–25
Filamentous algae (%)	0–25	0–25	0–25	0–25	0–25	0–25	0–25	0–25
Sand/gravel (%)	76	28	52	24	16	10	16	10
Cobbles (%)	14	54	38	68	22	28	34	20
Boulders (%)	10	18	10	8	62	62	50	70
Stream width (m)	3.9–10.6		2.6–7.3		3.2–9.1		1.8–7.2	
Stream depth (cm)	5–85		5–70		5–60		5–45	
Stream gradient (%)	1.9		3.6		14.3		29.3	
Water temperature ($^{\circ}\text{C}$)	13.0–22.0		14.8–20.8		17.0–25.3		18.8–24.6	
Conductivity (μScm^{-1})	30–32		25–29		26–31		32–36	
Dissolved oxygen (%)	75.3–92.2		68.4–89.9		83.4–99.2		83.5–97.7	
pH	5.61–7.40		6.78–7.33		7.37–8.40		6.40–8.10	
FRP ($\mu\text{g l}^{-1} \text{P}$)	4		4		3		3	
Nitrate + nitrite ($\mu\text{g l}^{-1} \text{N}$)	46		17		136		226	
Calcium (mg l^{-1})	<1		<1		<1		<1	
Magnesium (mg l^{-1})	<1		<1		<1		<1	
Sodium (mg l^{-1})	4		4		3		4	
Potassium (mg l^{-1})	<1		<1		<1		<1	

17.75°S, 145.61°E, 237 m) in the Tully Gorge National Park. The Paluma streams were located in relatively low-gradient upland headwaters and were slow-flowing (except during and after heavy rainfall), with shallow rocky riffles and runs, and some deep rocky pools; the Tully streams were high gradient, located at the base of mountains, and were generally fast-flowing with rocky riffles, cascades, waterfalls, runs and deep pools, and had a high proportion of large boulders (table 1). All streams flowed through rainforest (“simple notophyll vine forest” – Tracey, 1982) but the canopy was more open at Tully because of cyclone damage in February 2011. In Wet Tropics rainforests, maximum litter fall occurs in spring, but continues throughout the year, and accumulates in pools (Benson and Pearson, 1993). At Paluma, the pool substratum comprised mainly cobbles, gravel and sand, with substantial leaf litter accumulation. At Tully, the substratum consisted mainly of boulders and cobbles, with small patches of gravel and sand; leaf packs were sparse and accumulated only in the drier months when the water was shallowest. Runs and riffles had predominantly rocky substrata in all streams. Mats of filamentous algae were found in some stream pools at Tully, particularly during periods of low flow at sites with low canopy cover.

Survey methods

During 1989–94, sampling was carried out at varying intervals in riffles, runs and pools, along a 310-m transect. During 2011–13 we undertook monthly sampling in riffles and

pools only, along 150-m transects. These changes reduced sampling time and allowed all four streams to be sampled regularly. The data from the two survey periods were comparable as we used catch per unit effort to record tadpole abundance.

During 1989–94, we sampled two pools, two runs and three riffles along a 310-m transect in Birthday Creek. In 2011–13, we sampled three pools and three riffles along a 150-m transect in each of the four streams (except that during the first two months of sampling, we sampled two pools and two riffles in each Tully stream). The 2011–13 Birthday Creek transect was a 150-m subsection of the 1989–94 transect and the reaches sampled were again separated by stretches of different habitat type. The sampled reaches were assumed to be independent due to tadpoles’ distinct habitat preferences (Richards, 2002). We did not sample runs in 2011–2013 as they could not be defined during periods of faster flow. During the 1989–94 surveys at Paluma, we sampled at approximately two-weekly intervals between March 1989 and May 1991, monthly intervals between May 1991 and August 1992, and every two to three months between August 1992 and February 1994. During 2011–2013, we collected samples every four to six weeks at Tully and Paluma, commencing in October 2011 at Tully and in February 2012 at Paluma (delayed because cyclone damage prevented access).

In pools and runs, we sampled with rapid sweeps of a triangular-framed dip net (0.9×0.3 m mesh size) through

the water column; we “bounced” the net along the substratum and dislodged loose rocks to drive tadpoles into the water column, where they could be captured. In riffles, we sampled by rolling rocks to dislodge suctorial tadpoles, which were swept into the net by the current. During the 1989–94 surveys, we used five one-minute sampling episodes (sub-samples) in runs and riffles, and three 30-second episodes in each microhabitat in pools (i.e., total of 4.5 minutes). In the 2011–13 surveys, we used five one-minute episodes in each pool and riffle. We recorded catch per unit effort (per minute) as recommended for stream tadpoles (Shaffer et al., 1994).

We sorted and counted tadpoles in white photographic trays, and combined data from the subsamples. We measured tadpole body length to the nearest 1 mm using a ruler or calipers, after which we returned the tadpoles to the stream. During the 2011–2013 surveys, we wore vinyl gloves (Greer et al., 2009) at all times during sampling to avoid touching the animals directly, and changed gloves between habitats to minimise disease transmission (Greer et al., 2009).

We used data-loggers (Thermochron® iButtons) and maximum-minimum thermometers to record water temperatures. We used an Owen’s River Hydroprop to measure current velocity, and calculated the average velocity for each habitat from three readings, taken at locations likely to have minimum, maximum and intermediate velocities. We used a Hydrolab Quanta to measure pH, conductivity and dissolved oxygen in the streams at the time of sampling. We obtained monthly rainfall data for Paluma (6 km from the study sites) from the Australian Bureau of Meteorology, and for Tully from the Kareeya power station (10 km from Stream 1 and 5 km from Stream 2). Occasionally, daily rainfall was estimated from several days’ cumulative data.

Habitat data for the four streams were collected during the 2011–13 survey period. In September–October 2012, before the start of the wet season, we measured stream width and estimated substratum cover along the transects at 25-m intervals. We measured other variables during the regular surveys. We visually estimated canopy cover and leaf litter and filamentous algal cover of the substratum, as being within one of four quartiles for each habitat. We estimated minimum, maximum and mean depths for each stream from measurements at five points in each habitat, and stream gradient from elevation measures at the furthest downstream sampling site and 2 km upstream (using Google Earth®) as a descriptor of the nature of each stream. In the 2011–2012 summer, we collected water samples, which were analysed by the TropWater laboratory at James Cook University, to describe chemical characteristics of the streams (nitrate + nitrite, filterable reactive phosphorus (FRP), sodium, calcium, magnesium and potassium concentrations).

Data analyses

We analysed tadpole data from Paluma and Tully separately, but combined data for the two streams at each location, as abundance patterns were similar (supplementary fig. S2). Newly hatched tadpoles (size 1) were specifically identified

to indicate frog breeding periods. We categorised tadpoles as newly hatched when they had body lengths of 5.5 mm or less for *L. serrata*, 7.5 mm or less for *L. nannotis*, *L. rheocola* or *L. dayi*, and 10 mm or less for *M. coggeri*.

We used PRIMER 6 Version 6.1.15 and PERMANOVA+ Version 1.0.5 (Clarke and Gorley, 2006; Anderson et al., 2008) to carry out permutational MANOVA/ANOVA (PERMANOVA) of tadpole data. We compared total tadpole abundances for each species in 2011–2013 between locations and habitats, with habitat (pool or riffle) nested within location (Paluma or Tully). We compared total tadpole abundances among habitats for each species using one-way ANOVAs and, where appropriate, Tukey’s post-hoc tests ($\alpha = 0.05$) (Statistix 10 software, Tallahassee, Florida, USA). Similarly, to investigate the distribution of each species among current velocity categories at each location, we used ANOVAs and Tukey’s tests.

We analysed the relationships between the 2011–13 tadpole assemblages and environmental variables in R version 3.4.0 (R Core Team, 2017). We initially examined whether Poisson regression, zero-inflated Poisson regression, or negative binomial regression produced better fits using all candidate variables in full models. Poisson models were fitted using function *glm*; zero-inflated Poisson models were fitted using function *zeroinfl* in package PSCL (Zeileis et al., 2008); and negative binomial models were fitted using the function *glm.nb* in package MASS (Venables and Ripley, 2002). Only Poisson and negative binomial models were fitted to data from Paluma as no counts from that area were zero. We compared models using log likelihoods. These preliminary tests indicated that negative binomial regressions produced models that were better fits than Poisson or zero-inflated Poisson models, so we constructed models using negative binomial regressions of tadpole abundances on environmental variables. We used package *MuMin* (Bartoń, 2017) to carry out model selection and model averaging, using function *dredge* with AICc to choose the best fitting models or model sets, constraining the process to models with four or fewer parameters. When a model set was indicated, we used function *model.avg* to arrive at a final model using full averaging, and function *predict* to arrive at predicted values for the dependent variable. For all final models we calculated proportions of variance accounted for (r^2) by using the observed and predicted values of the response variable.

Results

Stream characteristics

Stream gradients were higher at Tully than Paluma and current velocity was therefore usually higher in Tully streams (table 1). Current velocity was lower in pools than in riffles ($H_7 = 279.4$, $p < 0.001$). Water temperatures were

up to 4.0°C lower on average at Paluma than Tully, corresponding with their different elevations. Overall, there were only minor differences in water quality between the two locations (table 1).

Tadpole abundance

Tadpoles of five frog species (*Mixophyes coggeri* and four species of *Litoria*) were collected (supplementary table S1). Tadpoles of *M. coggeri* were large (up to 92 mm total length), strong swimmers and typically found in pools; *Litoria* tadpoles were much smaller (36–62 mm) (Anstis, 2013). Those of *L. serrata* had non-suctorial oral discs, and inhabited pools; those of *L. dayi*, *L. nannotis*, and *L. rheocola* had strongly suctorial oral discs, and inhabited high velocity habitats. In the 2011–2013 samples, seasonal patterns of tadpole abundance differed significantly between the locations and between habitats within each location (respectively, pseudo- $F_{1,222} = 70.74$, $p < 0.001$; and pseudo- $F_{1,222} = 32.72$, $p < 0.001$). In Birthday Creek at Paluma, between 1989 and 1994, *Litoria serrata* (formerly included in *L. genimaculata*) and *Mixophyes coggeri* (formerly included in *M. schevilli*) were more abundant in pools or runs, whereas *L. nannotis* and *L. dayi* (formerly *Nyctimystes dayi*) were more abundant in riffles (fig. 1a). In the 2011–13 surveys, *L. serrata* and *M. coggeri* were found in the Paluma streams, but the other species were absent (fig. 1b). In the Tully streams, *L. nannotis* and *L. dayi* were most abundant in riffles, and *L. serrata* in pools, but *L. rheocola* tadpoles had similar abundances in the two habitats (fig. 1c).

At Paluma, all four species (when present) were most abundant in the summer months. There were distinct peaks of *L. serrata* tadpole abundance during summer in 1989–94, and in 2012–13 (fig. 2a). In most years, size-1 *L. serrata* tadpoles increased in abundance in September, and again in March or April, suggesting two breeding periods, or a prolonged breeding period with minimal recruitment during the central portion; this trend was particularly clear

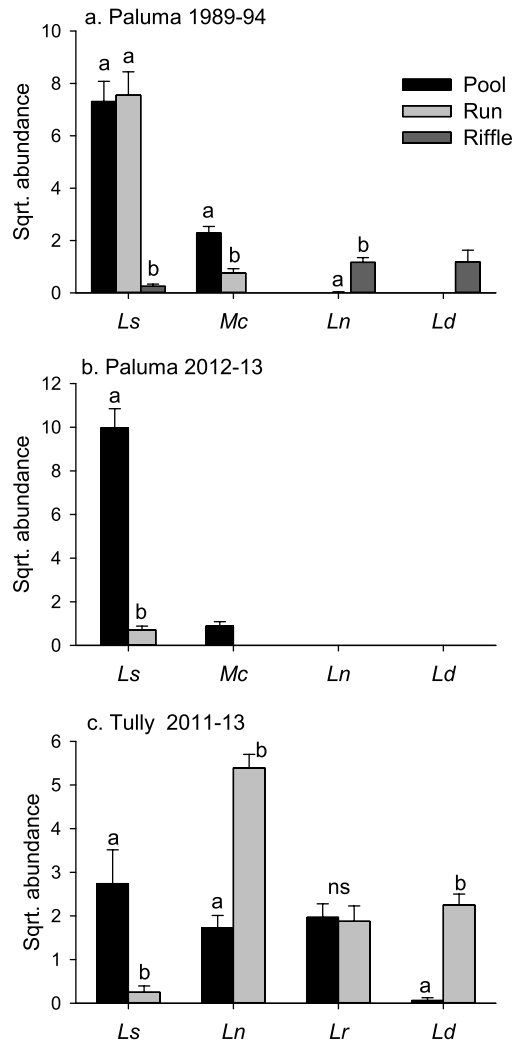


Figure 1. Square-root mean abundance per day (+ S.E.) for tadpoles of 4 frog species in streams at Paluma and Tully. (a) Paluma (Birthday Creek) 1989–94, pools, runs and riffles; (b) Paluma (Birthday and Camp creeks) 2011–13, pools and riffles; and (c) Tully (streams 1 and 2) 2011–13, pools and riffles. Within species, bars labelled with the same letter do not differ significantly (ANOVA, followed by Tukey's tests in (a), $\alpha = 0.05$); ns = not significant. Species are *Ld*, *L. dayi*; *Ln*, *L. nannotis*; *Lr*, *L. rheocola*; *Ls*, *Litoria serrata*; *Mc*, *Mixophyes coggeri*. ANOVA results: (a) d.f. = 2, 39; *Ld*, $F = 6.88$, $p = 0.003$; *Ln*, $F = 41.03$, $p < 0.001$; *Ls*, $F = 37.10$, $p < 0.001$; *Mc*, $F = 41.90$, $p < 0.001$; (b) d.f. = 1, 26; *Ls*, $F = 109.11$, $p < 0.001$; *Mc*, $F = 19.8$, $p < 0.001$; and (c) d.f. = 1, 26; *Ld*, $F = 72.56$, $p < 0.001$; *Ln*, $F = 75.77$, $p < 0.001$; *Lr*, $F = 0.04$, $p = 0.85$; *Ls*, $F = 10.12$, $p = 0.004$.

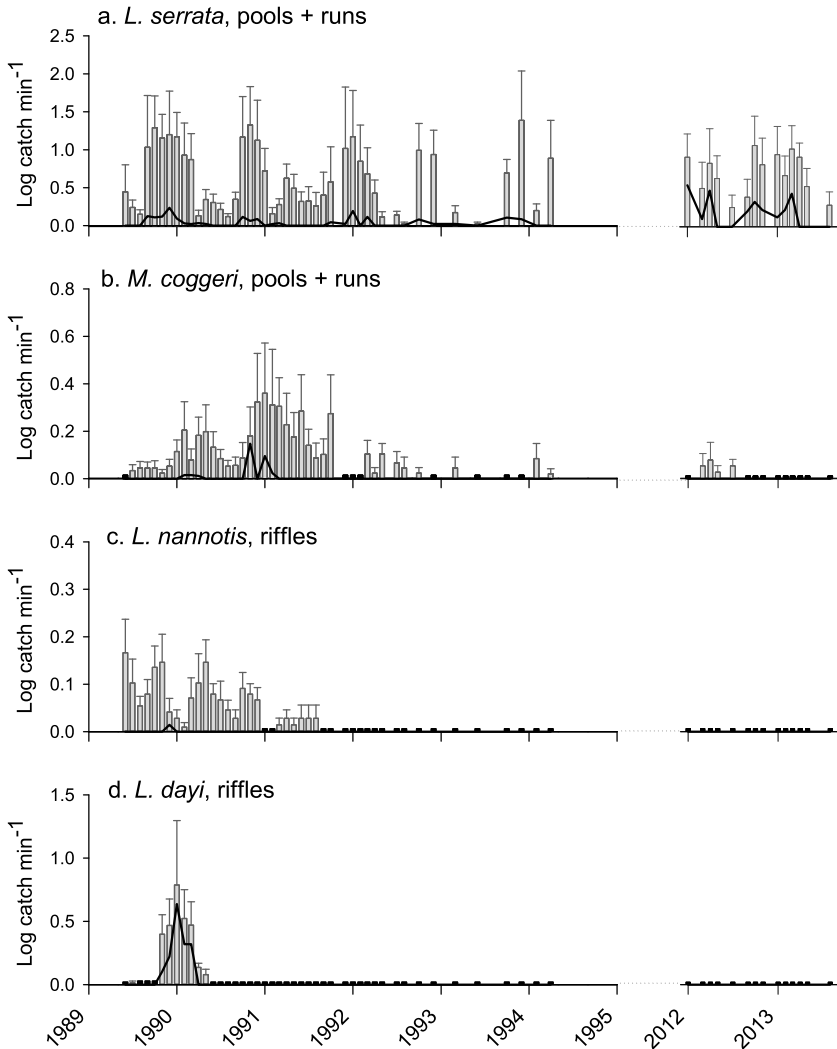


Figure 2. Tadpole catch per minute ($\log(x + 1) + \text{SE}$) of all tadpoles (bars), and size-1 tadpoles (lines) at Paluma (Birthday Creek) between June 1989 and May 2013, with a gap in sampling between April 1994 and October 2011. The short black bars represent samples with zero animals.

in 2012-13. *Mixophyes coggeri* tadpoles were most abundant in late 1990 and early 1991, and were much less abundant over the second half of the first survey period and in 2012-13 (fig. 2b). Size-1 *M. coggeri* tadpoles were present intermittently throughout 1989-94, with a peak in November 1990. There were two abundance peaks for *L. nannotis*, in early and late summer, but there was no recruitment of *L. nannotis* tadpoles after 1989 and all tadpoles of this

species disappeared from the stream by the end of 1991 (fig. 2c). *Litoria dayi* tadpoles (including size 1, the new recruits) peaked in abundance in January 1990, but numbers dropped to zero by mid-1990 (fig. 2d).

In the Tully streams, tadpole abundances were also highest in the warmer months, but reached abundance maxima at different times: *L. serrata* and *L. rheocola* in spring and early summer (figs 3a and 3c respectively); *L. nan-*

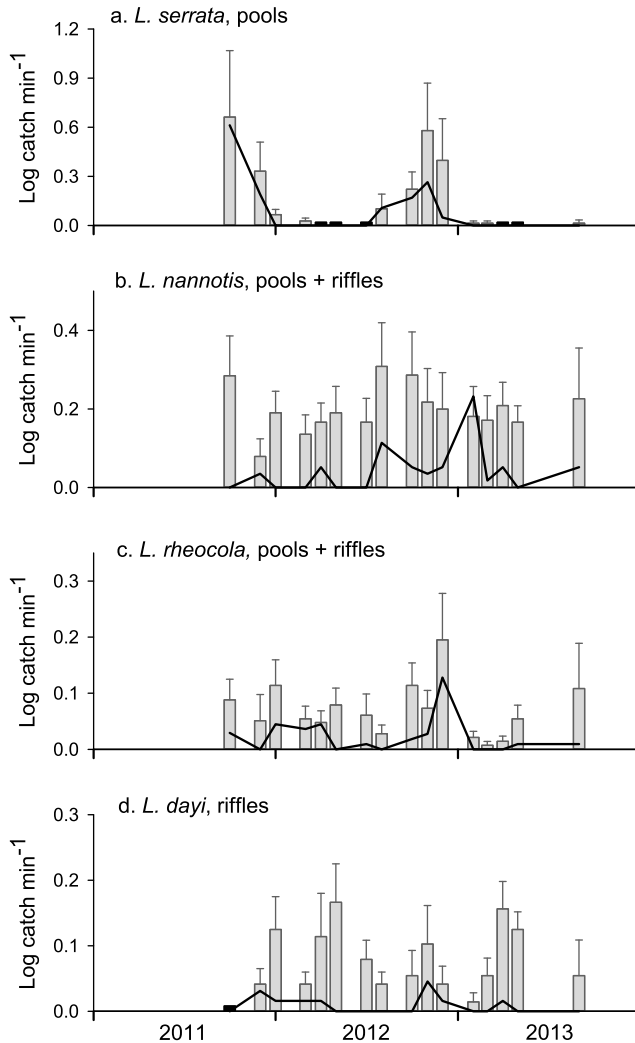


Figure 3. Tadpole catch per minute ($\log(x + 1) + \text{SE}$) of all tadpoles (bars), and size-1 tadpoles (lines) at Tully (streams 1 and 2) between October 2011 and May 2013. The short dark bars represent sampling periods with no animals. Estimates for September 2013 are based on stream 2 only.

notis between late winter and spring (fig. 3b); and *L. dayi* in spring or late summer, depending on the year (fig. 3d). *Litoria rheocola* and *L. dayi* were not present in large numbers and had no distinct peaks. *Litoria serrata* had a distinct breeding period at Tully, whereas small tadpoles of *L. nannotis* were present throughout spring and most of summer. Tadpoles of all four species were present in the streams all year but decreased in abundance over winter.

Influence of environmental variables

For all analyses at both locations, the initial full models incorporated effects of water temperature, percent canopy cover (> 10 m height), percent cover of the substrate by leaf litter, and the natural logarithms of current velocity (ms^{-1}) and of total rainfall ($\text{mm} + 1$) in the previous 1, 3, 7, and 14 days. We used log transformations to render these data less skewed and more platykurtic. Table 2 summarises the re-

Table 2. Results of model selection for effects of environmental parameters on tadpole abundances. Intercepts are shown as having weights of 1, as all models include them. – indicates that a parameter is not in a model or averaged model. Supplementary table S2 shows the top 20 models in each model set.

	Intercept	Algal cover	Canopy cover	Log(current velocity)	Litter cover	Log(14 day rainfall)	Log(1 day rainfall)	Log(3 day rainfall)	Log(7 day rainfall)	Water temperature
Paluma <i>L. serrata</i>, average of top 14 models, $R^2 = 0.162$										
Parameter weight	1.00	0.10	0.57	1.00	0.16	0.11	0.12	0.10	0.10	1.00
Averaged model	0.19310	0.00046	-0.00329	-16.54000	0.00066	-0.01034	0.02273	-0.00139	-0.00581	0.16160
Tully <i>L. serrata</i>, average of top 13 models, $R^2 = 0.389$										
Parameter weight	1.00	1.00	0.11	1.00	0.16	0.12	0.44	0.63	0.12	0.11
Averaged model	1.31900	0.01976	-0.00018	-14.71000	0.00427	-0.01941	-0.49050	-0.66620	0.01439	0.00118
Tully <i>L. dayi</i>, average of top 16 models, $R^2 = 0.371$										
Parameter weight	1.00	0.39	1.00	1.00	0.07	0.14	0.14	0.19	0.59	0.06
Averaged model	0.55210	-0.01066	-0.01084	8.65200	-0.08485	-0.03145	-0.03714	-0.04817	-0.23700	0.00186
Tully <i>L. nannotis</i>, first model $R^2 = 0.160$										
Parameter weight	1.00	1.00	-	1.00	1.00	1.00	-	-	-	-
First model	3.81733	-0.01937	-	3.17141	-0.08800	-0.52619	-	-	-	-
Tully <i>L. rheocola</i>, average of top 9 models, $R^2 = 0.160$										
Parameter weight	1.00	0.39	0.14	0.69	NA	0.67	0.93	0.87	0.13	-
Averaged model	1.00076	-0.00498	-0.00094	-2.09766	NA	-0.66287	-1.72115	1.50473	0.14222	-

sults of our model selection analyses; full details are given in supplementary table S2. The abundance of *L. serrata* tadpoles in the Paluma area was most strongly influenced by the negative effect of water flow and canopy cover, and the positive effect water temperature. The effects of algal cover and rainfall were lightly weighted, indicating that their effects on predicted abundance were weak. The calculated r^2 of 0.162 indicates that a large proportion of the variability in abundance of *L. serrata* tadpoles was not explained by the environmental effects measured in this study.

At Tully, the abundances of *L. serrata* were affected by all of the measured environmental parameters. As at Paluma, the effects of flow rate were strong, consistent, and negative, but unlike Paluma, the effects of water temperature were weak. The effect of canopy cover was weaker at Tully, while the effect of algal cover was strong, consistent and positive. Antecedent 1-day and 3-day rainfall had negative effects.

At Tully, *L. dayi* tadpoles were most strongly affected by current velocity and 7-day rainfall (positively), and canopy cover and cover of attached algae (negatively). For *L. nannotis*, the

single best fitting model was clearly the most adequate, so we did not perform model averaging. The effects of 14-day rainfall, algal cover and litter cover were negative, while the effects of current velocity were strongly positive. *L. rheocola* tadpoles were most strongly affected by current velocity and 1-day rainfall (negatively), and 3-day rainfall (positively).

The results of the modelling with respect to current velocity are mirrored in fig. 4. *L. serrata* tadpoles occurred at low velocities. *Litoria rheocola*, *L. nannotis* and *L. dayi* tadpoles were found at increasingly higher velocities.

Discussion

Our models identified several variables that affected tadpole occurrence in Wet Tropics streams, generally consistent with their known biology. Current velocity was the most important influence on the tadpole assemblages, with all four species we modelled showing distinct habitat preferences, most likely due to adaptations to and tolerance of strong currents (e.g., suctorial mouthparts; Richards, 2002). Water

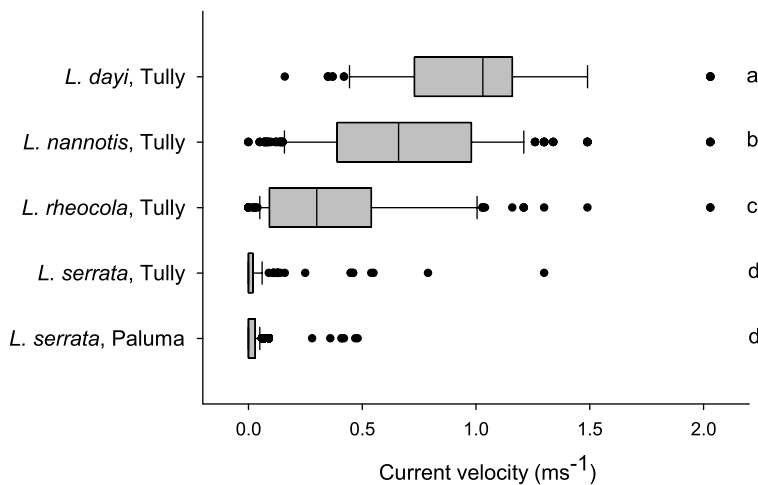


Figure 4. Distribution of tadpoles of 4 frog species over a range of current velocities during the 2011-2013 surveys at Paluma and Tully. The lower, middle and upper boundaries of the box represent the 25th, median and 75th percentiles, respectively, of velocities at which at least one tadpole was found in a sample. Whiskers represent the 10th (lower) and 90th (upper) percentiles and dots, other data. Bars labelled with the same letter do not differ significantly (ANOVA, d.f. 4, 2464; $F = 1213.3$, $p < 0.001$; followed by Tukey's tests, $\alpha = 0.05$).

temperature was a strong influence at Paluma, reflecting the seasonal breeding patterns, but had little effect at Tully, probably because the lowland streams experienced lower seasonal fluctuations and higher minimum temperatures. Antecedent rainfall, which relates directly to flow (Clayton and Pearson, 2016), had some influence on the assemblage at Tully, but very little at Paluma, reflecting the generally faster flow at Tully. Canopy cover was generally more important at Paluma, where it was greater. Algal cover appeared to be important (both positive and negative effects) at Tully, but not at Paluma, where algal cover was generally sparse, but litter cover tended to be high. Abundant filamentous algae can reduce tadpole density (Wahbe and Bunnell, 2003), which may explain the negative relationship between riffle-dwelling tadpole abundance and algal cover at Tully; however, this relationship probably also reflects the flow environment, as algal cover was inversely related to current velocity. Unexplained variation in the models (61–84%) was probably partly caused by our variables not capturing every aspect of the environment of importance to tadpoles, and partly by tadpoles' wide habitat tolerances (Cashins, 2009).

Tadpole abundances at Paluma were most likely directly affected by the collapse of the adult breeding populations of *L. nannotis* and *L. dayi*, associated with chytridiomycosis (Richards et al., 1993; Berger et al., 1998; McKnight et al., 2017), during the period in which amphibian losses occurred throughout the Wet Tropics uplands (Richards et al., 1993; McDonald and Alford, 1999) (the prevalence of infection by *B. dendrobatidis* was not measured in this study). Both species were absent from the area in 2012–13, indicating that the species had not recovered (McKnight et al., 2017). Pool species continued to be present at Paluma during and after the decline period. *L. serrata* adult populations recovered (Woodhams and Alford, 2005) and our results indicate that the abundance of *L. serrata* tadpoles was similar across survey periods. Tadpoles of the other

pool species at Paluma, *M. coggeri*, decreased in abundance over this period, suggesting limited recruitment. However, there is no published evidence for any decline of this species and populations have been recorded as stable (Richards et al., 1993; Williams and Hero, 1998; McDonald and Alford, 1999). Nevertheless, the low abundance of *M. coggeri* tadpoles recorded during the 2012–13 surveys, strongly suggests that the population breeding in streams at Paluma had declined. Elsewhere in eastern Australia, *Mixophyes fleayi* populations initially decreased during amphibian declines, then recovered over a seven-year period (Newell et al., 2013). It is possible that the trajectory of *M. coggeri* at Paluma is following a similar, though slower, course.

Tadpoles recorded in the Tully streams during the 2011–13 surveys were of the same species as those recorded in the lowlands before amphibian declines (C. Hoskin, pers. com.). *Litoria nannotis* and *L. dayi* did not disappear at Tully as they did at Paluma, although they may have declined. However, our results are consistent with the observation that chytridiomycosis has greatest impact in the cool uplands (McDonald and Alford, 1999; McKnight et al., 2017).

Overall, tadpole abundance was highest in spring and summer, following recruitment. Abundances of the various species peaked at different times, possibly reducing competition within habitats (Altig and Johnston, 1989; Bertoluci and Rodrigues, 2002). The timing of the breeding peaks of *L. serrata*, *L. nannotis* and *L. dayi* differed between Paluma and Tully, probably due to temperature differences (Afonso and Eterovick, 2007), with winter temperatures being higher at Tully than Paluma because of the ~600 m difference in elevation. Likewise, variation between years probably resulted from differences in rainfall, stream flow and temperature.

Large tadpoles of all species were present throughout most winters, presumably maturing in the warmer months. Tadpoles at Tully typically hatched in spring or summer, underwent

most growth and development over winter, and then metamorphosed the following spring or summer (Cashins, 2009; Sapsford et al., 2018). Similarly, at Paluma, large *M. coggeri* tadpoles appeared to remain in the stream over winter and metamorphose in spring or summer. Prevalence of *B. dendrobatidis* infection in both tadpoles and terrestrial frogs tends to increase over winter (Sapsford et al., 2018), and newly metamorphosed frogs of some species can have high intensities of infection (Vredenburg et al., 2010). However, metamorphosis in the late spring and summer months may reduce the risk of development of chytridiomycosis as environmental temperatures and individual body temperatures are more likely to reach levels outside the range optimal for the pathogen (Rowley and Alford, 2013). The emergence of chytridiomycosis might have selected for later summer metamorphosis; however, there was no evidence that the timing of metamorphosis changed following amphibian declines at Paluma.

Our results show that spatial and temporal fluctuations in tadpole populations were partly controlled by a few habitat and climatic variables, along with the likely impact of chytridiomycosis. The tadpole assemblages observed during this study indicated that the riffle species at Paluma disappeared from the stream during the first survey period at the same time as adult frogs disappeared and remained absent, whereas the pool species showed signs of recovery and remained present during both survey periods. The decline and loss of tadpoles during the 1990s clearly shifted food web patterns in riffles (Schmidt et al., 2017). Therefore, the changes in the seasonally high abundances of tadpoles at upland sites are likely to have substantially influenced the overall stream assemblage composition and trophic processes.

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Supplementary material. Supplementary material is available online at:

<https://brill.figshare.com/s/781559b2d4eca74f0353>

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